

Behavior and Ecology of *Acanthoscelides prosopoides*¹

(Coleoptera: Bruchidae)

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The attacks of the larvae of the seed beetles or Bruchidae on plant seeds are of importance because commercial peas and beans are commonly destroyed. Since many non-economic Leguminosae are attacked as well as the seeds of some 27 other plant families, bruchids may be utilized in the future to destroy the seeds of weeds. The destruction of seeds is initiated when adult females oviposit into or on the seeds or pods and the larvae then hatch and burrow into the seeds. In most species, the larvae feed, moult several times, and then pupate inside seeds but some are known to construct silken pupal chambers inside pods or in the ground. The adult then emerges from its pupal chamber through a typical circular bruchid exit hole. The adults may or may not feed prior to mating and oviposition.

When Schaeffer described *Bruchus prosopoides* in 1907 he mentioned its close resemblance to *Bruchus prosopis* LeConte, hence the name. Knowledge gathered in the last 60 years indicates these two species resemble one another only superficially and consequently *B. prosopoides* is now placed in the genus *Acanthoscelides* and *B. prosopis* in the genus *Algarobius*. Host plant preferences are criteria also used to separate the two. *Algarobius prosopis* is known to breed only in the seeds of species of *Prosopis*. *Acanthoscelides prosopoides* larvae feed in the seeds of *Ziziphus obtusifolia* (Hooker) A. Gray, family Rhamnaceae.

The affinities and nomenclature of the spiny shrub called lotebush or *Z. obtusifolia*, have been confused for many years. The name *Condalia lycioides* (A. Gray) Weberbauer has frequently been used for this species but Johnston (1962, 1963) removed it from the genus *Condalia* and adopted the senior synonym *Z. obtusifolia*. We will follow Johnston's usage in this paper.

The first rearing of *A. prosopoides* was reported by Johnson (1970) from information on a specimen borrowed from the U. S. National Museum of Natural History. The specimen was reared from seeds of *Z. obtusifolia* collected on 18 May 1954 at Brownsville, Texas by an unknown collector. Johnson also reported a rearing from seeds he col-

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lected at Quitobaquito, Organ Pipe National Monument, Pima County, Arizona on 14 April 1968. The distribution of the insect (Johnson, 1970) and plant (Johnston, 1963) is from southeastern California to southern Oklahoma and south into Mexico.

Since over 80% of the bruchid species whose host plants are known attack seeds of the Leguminosae and most species of *Acanthoscelides* attack papilionaceous legumes, the ecology and behavior of the unique *A. prosopoides* were studied and are reported upon here. It is hoped that this knowledge will aid in understanding the phylogeny of this species and therefore other species in the genus.

The mature fruit of *Z. obtusifolia* is a drupe 7–10 mm in diameter with a thin exocarp, a fleshy mesocarp, and a woody endocarp. Although the endocarp contains two seed chambers, usually only one seed and one seed chamber are enlarged.

During the study mature fruits were collected once weekly from 5 May 1969 to 30 June 1969 from about 5 miles south of Camp Verde, Yavapai County, Arizona. Collecting was discontinued after 30 June because only occasional fruits were encountered.

Most of the fruits had turned to the dark blue color of maturity by 6 June. The only apparent difference between these and the fruits collected to 30 June was a slow desiccation of the flesh surrounding the stones although in the last sample the flesh was moist and reasonably soft. Large numbers of fruits were found on the plants until 18 June when a decrease was noted. The numbers declined rapidly so that after 30 June hardly any fruits were to be found on the plants. Therefore, during June the bruchids had an abundant supply of acceptable fruits for oviposition.

Mature fruits were brought to the laboratory and treated according to the methods of Bottimer (1961) and Johnson (1968, 1970). The results of our studies are presented and discussed below.

MATING BEHAVIOR

There were two types of responses exhibited by the male in the presence of a female. Frequently the male approached a female from the rear and quickly climbed onto her back. When the female raised her abdomen, the male backed up slightly and copulation occurred immediately.

Also a male approached a female from the rear and stimulated her pygidium with a short series of quick nudges produced by the up and down movement of the male's head with the mouthparts touching the

female. He then stimulated the apex of her elytra and sometimes up to the distal one-fourth of the elytra. As the male progressed up the female's elytra, his anterior legs grasped the sides of the pygidium, abdomen or elytra, depending on the height and relative size of the two insects. This usually continued for about three to five minutes. On some occasions the female was observed to walk away, although she remained in the immediate area. The male either followed or stayed in place nudging at the substrate. When the male was apparently ready for copulation he quickly attempted to find and mount a female as described earlier.

Apparently this stimulation affects only the male's readiness for copulation. During the mating ritual, if other females were near, an-

During copulation the male's lateral lobes became extended as the median lobe entered the female. When the median lobe was fully inserted the lateral lobes were at their maximum ventral extension. During other female sometimes appeared to offer herself in place of the original. In each thrust the lateral lobes appeared to grasp the exposed sides of the pygidium and then relax.

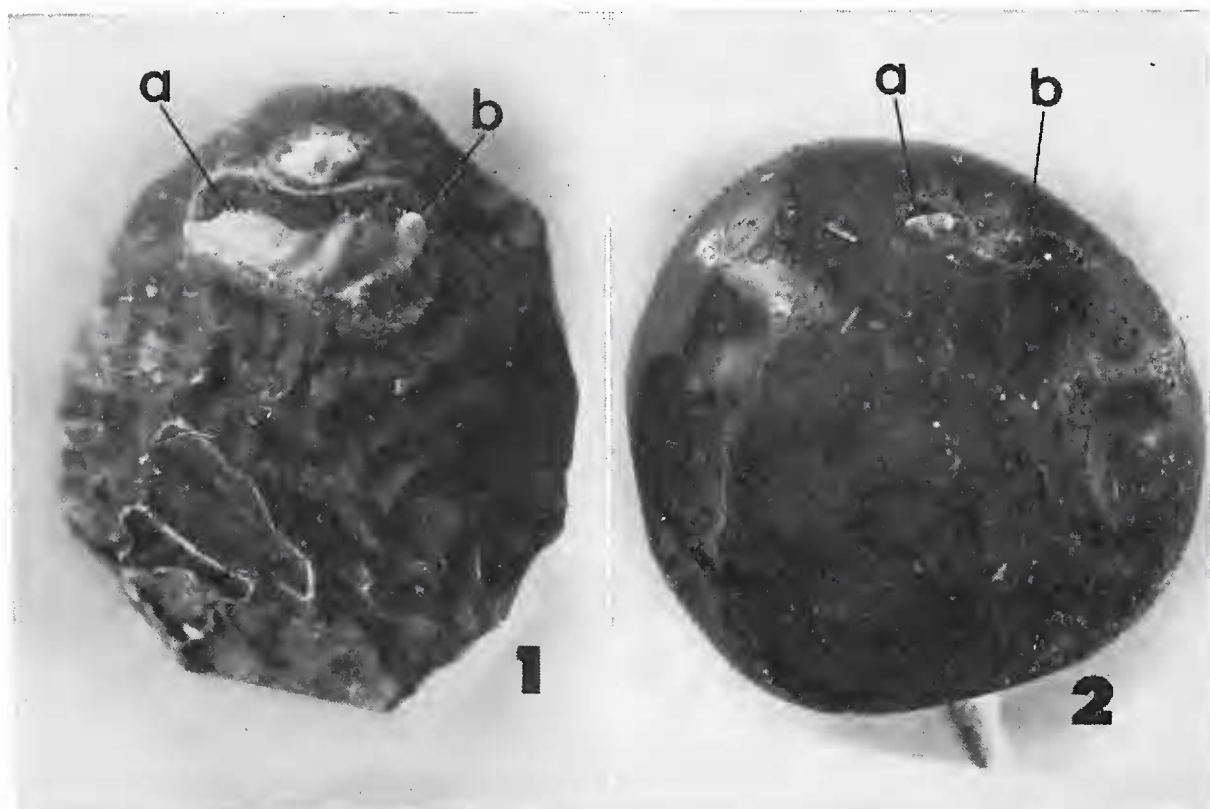
During copulation the male cleaned his legs and antennae with his free legs while perpendicular to the substrate with his hind legs balancing him. The female also appeared to preen herself. Unless disturbed, it seemed that the male was the one to discontinue copulation.

Food is not a necessary prerequisite for copulation or for production of viable eggs. Although adults were observed to feed on the flesh of the host fruit in the laboratory, the teneral adults taken from isolated fruits copulated within minutes after being placed in a petri dish without ever being exposed to food or water. The females then laid viable eggs.

OVIPOSITION

Eggs of *A. prosopoides* were observed to be deposited on two different areas of the fruits collected and isolated in May and June. When holes were present in the flesh of the fruits (Fig. 1 a), eggs (Fig. 1 b) were laid and cemented into them. The holes were probably the result of the fruits being struck by spiny branches. The most common area selected was next to the atrophied style (Fig. 2 a). This type of egg deposition was most common in the field collected material because the exocarp of the fruits in the field rarely exhibited cracks and holes while on the plant.

In the laboratory both of the above methods were observed in cul-



FIGS. 1-2. *Ziziphus obtusifolia* fruit. FIG. 1. a. Hole in flesh. b. Egg of *Acanthoscelides prosopoides* laid in hole. FIG. 2. a. Egg of *Acanthoscelides prosopoides* laid near remnants of the style. Note larval exit hole on the right, ventral surface of the egg. b. Exit hole of an adult *A. prosopoides*.

tures. When recently emerged *A. prosopoides* adults were allowed to remain with the fruits in the jars, eggs were found laid in cracks and holes in the fruit. Most often the holes utilized were those remaining when the pedicel separated from the fruit. Also eggs were sometimes laid on any part of the surface of the fruit and even on twigs. We believe this behavior to be due to the crowded conditions of the laboratory since eggs were not observed to be deposited in this manner in the field.

Eggs and first instar larvae of *A. prosopoides* were easily obtained by allowing the females to oviposit into open-celled styrofoam. They seemed to prefer these holes to holes in the flesh of the fruit or to the surface of the fruit. The presence of a fruit suitable for oviposition does not seem to be the primary stimulus for egg deposition. Rather, it would appear that *A. prosopoides*, like many other bruchids, will oviposit when given the correct physical stimuli. It appears an appropriate hole triggers oviposition regardless of the surrounding material.

Further observations of this species are necessary to discover if eggs are laid on other seeds or surfaces in the field and to reveal the other stimuli for oviposition.

TABLE 1. Emergence of *A. prosopoides* from isolated fruits of *Z. obtusifolia* in 1969.

Culture #	1	2	3	4	5	6
Date Coll.	29 May	6 June	10 June	18 June	24 June	30 June
# of fruits	42	374	376	241	118	122
# infested	3	28	20	9	6	20
% infested	7.2%	7.5%	5.3%	3.8%	5.1%	16.4%

IMMATURE STAGES

EGG CHARACTERISTICS.—Unlike bruchids which infest the seeds of some other large plants in the area, *A. prosopoides* eggs are not cemented with one side flat against the surface of the seed coat or pod. Rather the middle of the egg is cemented and the ends protrude from the substrate. The egg of *A. prosopoides* has a smooth chorion, is about 0.75 mm long, and is 0.31 mm at its widest.

FIRST INSTAR LARVA.—The first instar larva exits near one end of the egg adjacent to the fruit surface and does not burrow directly from the egg into the fruit as many bruchids do. Usually eggs are laid next to the atrophied style in the field (Fig. 2 a). The exit hole is in the anterior end of the egg and the hole produced by the entering larva is near the egg. The adult emergence hole (Fig. 2 b) is also usually near the style.

Although it would seem more advantageous for the larvae if the eggs were laid in protected cracks, the majority of infested field-collected fruits had eggs laid on their exterior. This could be a result of collecting fruits only from the plant. As fruits were rarely found on the ground, we suspect that they were probably removed by other animals such as rodents or birds.

DEVELOPMENTAL TIME

Observations in the laboratory indicated that the average time between copulation and egg deposition was two days for teneral females. An average of five days was required for the development of first instar larvae from the time of oviposition to eclosion.

The maximum developmental time from first instar larva to adult was 82 days. In the isolated cultures about 4% emerged after 60 to 80 days. This delayed development of a small percentage may be normal, creating overlap between summer generations.

Culture Examination Date		June (VI)				July (VII)				August (VIII)				Sep. (IX)											
Culture No. and Coll. Date		14	16	22	26	30	4	8	12	16	20	24	28	1	5	9	13	17	21	25	29	2	6	10	-----29
1 V-29	A																								0
	B	C																							I
2 VI-6	A	2,	2,	3,	1,	8,	9,	11,	6,	0,	51,	14,	30,	7,	9,	17,									
	B	2, 2, 2, 5, 4, 6, 2, 2, 3,																							
3 VI-10	A	2,	2,	1,	3,	3,	3,	0,	0,	8,	4,	2,	17,	4,	0,										
	B	1, 1, 6, 2, 4, 2, 1, 1, 1,																							
4 VI-18	A			1,	4,	5,	4,	8,	3,	13,	21,	46,	40,	44,											
	B			2,	1,	1,	1,	2,	1,	1,															
5 VI-24	A				5,	11,	9,	12,	25,	26,	36,	134,	62,	73,	37,										
	B				1, 1, 1, 1, 2,																				
6 VI-30	A					0,	0,	0,	1,																0
	B					1, 1,	1,	1,	2,	9,	3,	1,													
Ziziphus obtusifolia		---Fruit present---X-----Flowering-----																							

FIG. 3. Emergence data of *Acanthoscelides prosopoides* reared from jar and isolated cultures of *Ziziphus obtusifolia*.

PERCENT OF SEEDS INFESTED

After the insects had ceased to emerge from the seeds, the percent of the fruits destroyed was calculated (Table 1). Although an unknown number of fruits contained two seeds, the fruit was treated as a unit because in only one instance (culture 6) did two adults emerge from one fruit. However, only one seed was used by an *A. prosopoides* larva in the course of its development.

There was a dynamic increase in percent infestation in the 30 June collection (Table 1). Possible causes for this sudden increase is that fewer fruits were available and more insects may have been present than earlier in the season. Both could lead to oviposition of more eggs on the available fruits.

LIFE CYCLE AND GENERATIONS PER YEAR

On 14 April 1968, some fruits of *Z. obtusifolia* were collected at Quitobaquito, Organ Pipe National Monument, Pima County, Arizona. Some of these were isolated in gelatin capsules and the rest were stored in a pint fruit jar. Both the isolated and jar cultures were examined periodically for emerged adults. During March 1969 some of these fruits were dissected and overwintering *A. prosopoides* larvae were found in them. No adults had emerged from seeds in the culture since they were last examined on 17 December 1968. All of the larvae were

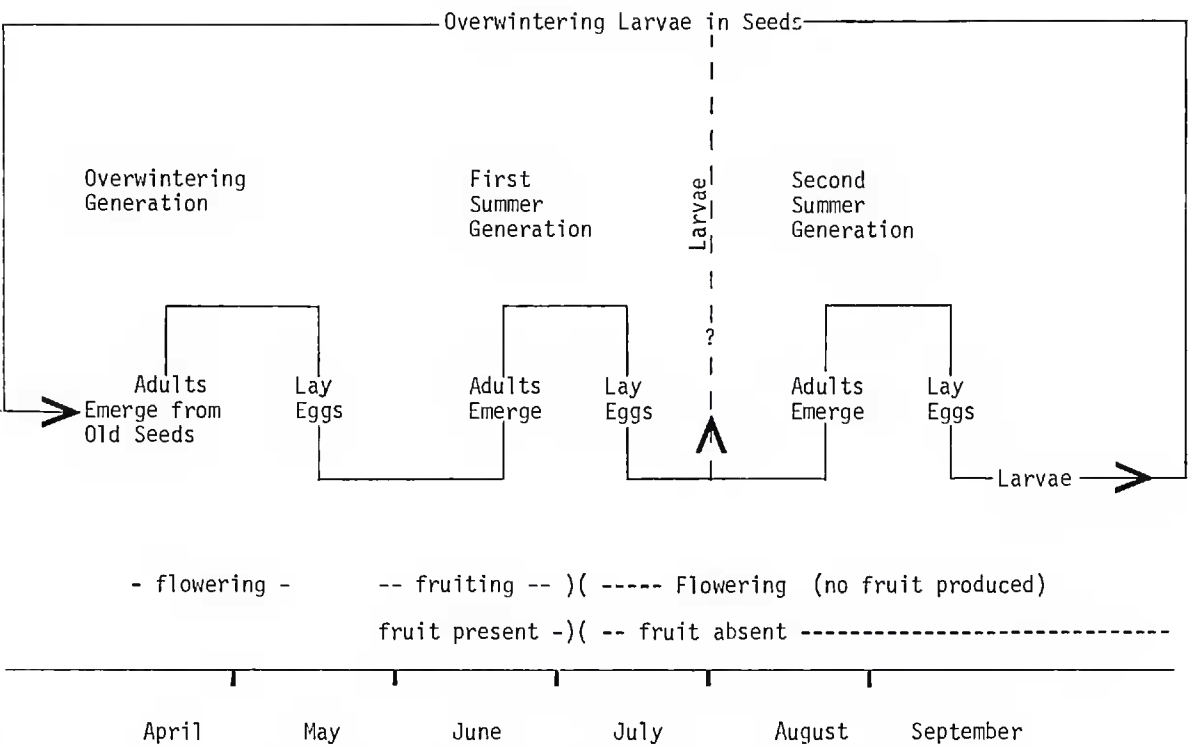


FIG. 4. Proposed life cycle of *Acanthoscelides prosopoides*.

of equal size and appeared ready to pupate. The adults started to emerge by 21 May 1969. As adults have been collected on these plants in nature as early as 14 April in some areas, the development of these insects may have been slowed because the culture was kept under laboratory conditions at room temperatures. However, it appears that the developmental time of the bruchids had not been altered significantly. In isolated seeds of this culture no adults emerged in the summer of 1969.

In Fig. 3 the number of *A. prosopoides* that emerged from the jar cultures and the isolated cultures are listed. The date that each culture was collected is indicated under its number and with cultures 3–6 is also indicated by a solid vertical line.

Culture 1 consisted of immature fruits. However, *A. prosopoides* were able to complete their development within the small seeds. Small fruits collected one week earlier did not yet have fully developed seeds inside them and the only insects which emerged from the latter seeds are in the wasp family Pteromalidae, probably parasites of lepidopterous larvae.

The last adult emerged from the isolated fruits of culture 2 on 21 July 1969, yet *A. prosopoides* continued to emerge from fruits in the jars for approximately another two months. The end of emergence from the isolated fruits coincides with the emergence of adults from fruits in the jar cultures. This is strong support for a theory that there are at least two generations of adults produced during the summer months

(Fig. 4). If there are indeed two generations plus the generation that overwinters and emerges in May, then there are three generations per year. It would seem reasonable that the second summer generation lays the eggs of the overwintering generation (Fig. 4).

However, the adults of the first generation possibly lay two types of eggs; one that gives rise to the second generation plus one that produces the overwintering larvae (Fig. 4, dashed line).

Culture 3 has the same general characteristics as those explained for culture 2, except the period of time between the two generations is longer. The one late emergence recorded from the isolated culture is an example of the variation in larval developmental time discussed earlier. This variation could cause an overlap between the two generations.

Cultures 4 and 5 apparently were collected late enough so that variation may have eliminated any diphasic emergence pattern that was present in cultures 2 and 3 or they were collected late enough so that eggs laid by both the overwintering generation and the first summer generation were present.

Culture 6 is important for two reasons. 16.4% of the fruits were infested which is 2 to 4 times greater than infestations in cultures 1–5 (Table 1), and it was the last culture to be collected. Almost all of the fruits were isolated and few adults emerged from the jar cultures. The higher infestation rate in this culture may be a direct result of a combination of an increased number of adults in the field and a reduction in the number of fruits tending to concentrate eggs on the fruits remaining on the plant.

Most plants had fruits remaining on them probably no later than one or two weeks after the last collection. Thereafter, some started flowering and continued to flower for the rest of the summer but without fruiting again. Consequently, several problems arise while trying to interpret the emergence data (Fig. 3).

Since three generations per year are apparent in the laboratory, we can only assume the same occurs in the field. We believe this assumption is valid because there is no evidence that emergence continues throughout the year as it does with some species which breed continuously as do *Stator limbatus* (Horn) and *Acanthoscelides obtectus* (Say). Also the time of emergence in the laboratory of the overwintering generation roughly corresponds with the time fruit is available in the field.

If developmental times are not significantly influenced by laboratory conditions and temperatures, as suggested earlier, then the majority of the first and all of the second generation emerge when there are no

more fruits available on the plant for oviposition for the second and/or overwintering generation. If eggs were laid for the second summer generation before the fruits disappeared from the plants, where were the fruits when *A. prosopoides* emerged? They were not on the plant, nor were any discovered on the ground. It is possible that rodents collected the fruits and stored them where *A. prosopoides* of the second generation could emerge and lay eggs for the overwintering generation. If this is not the case, then the first generation adults would have had to have laid two different types of eggs, one kind for the second generation and another for the overwintering generation.

EFFECT OF *A. PROSPOIDES* ON THE REPRODUCTIVE BIOLOGY OF *ZIZIPHUS OBTUSIFOLIA*

Although the maximum percentage of seeds destroyed in any culture in this study was 16.4 (Table 1), it appears that a second generation and other seed-eating animals in the area would have a significant effect on the number of viable seeds that survive in any one year. Apparently some protective mechanism yet to be discovered is possessed by this plant species to prevent attacks of bruchids on its seeds. Or, as this bruchid species appears to have only recently adapted to this plant, it has not yet evolved the ability to fully exploit the seeds of *Z. obtusifolia*. Many crops of legume seeds are almost completely destroyed by bruchids.

ASSOCIATED HYMENOPTERA

The eggs, larvae, and pupae of many bruchids which feed in the seeds of the Leguminosae are attacked by hymenopterous parasites, sometimes to the extent that almost all the beetles are destroyed. However, in our cultures containing *A. prosopoides*, only occasional bruchids were parasitized.

Eupelmus cushmani (Crawford) and an unidentified species of *Eupelmus* were reared from fruits of *Z. obtusifolia* from 5 miles south of Camp Verde. Although Peck (1963) reported *E. cushmani* as a parasite of the bruchids *Acanthoscelides ochraceicolor* (Pic) and *Mimosestes sallaei* (Sharp) as well as one species of Platystomidae and six species of Curculionidae, dissections of these fruits revealed only an empty, undamaged, pupal exoskeleton of *A. prosopoides*.

Several specimens of two as yet unidentified species in the family Pteromalidae were also reared from fruits collected 5 miles south of Camp Verde. Dissections of fruits from which they emerged revealed the remains of both *A. prosopoides* larvae and pupae. The other ptero-

malid, *Pseudocatolaccus americanus* Gahan, was reared from seeds from Quitobaquito and is probably not a bruchid parasite as Peck (1963) listed it as attacking species of Cecidomyiidae.

Several specimens of *Urosigalphus bruchi* Crawford (Braconidae), a parasite of the immature stages of the bruchids *Amblycerus robiniae* (Fabricius) and *Algarobius* sp. (Muesebeck et al., 1951), were reared from seed cultures from both localities, but we have no direct evidence that it is also a parasite of *A. prosopoides*.

The lack of appreciable numbers of parasites in our cultures indicates that *A. prosopoides* probably evolved the habit of attacking the seeds of *Z. obtusifolia* not only because of their nutritional value but also because of the few parasites which prey upon them when in the seeds of *Z. obtusifolia*. The small number of parasites also suggests a rather recent adaptation to these seeds by *A. prosopoides*.

The other Hymenoptera reared from our cultures are not known to be bruchid parasites. *Galeopsomopsis transcarinata* Gahan, a species which we reared from seeds collected at Quitobaquito, is listed by Peck (1963) as attacking the Cecidomyiidae. *Paragaleopsomyia eja* Girault, reared from both localities, has no known hosts but its relative, *P. gallicola* Gahan, is listed by Peck as attacking the Cecidomyiidae. We reared an unidentified species of *Torymus* from seeds collected at Quitobaquito. Peck lists species of *Torymus* as attacking a variety of hosts.

Eurytoma squamosa Bugbee was reported by Bugbee (1967) to attack the seeds of five species of *Ceanothus*. We reared this species only from seeds collected at Quitobaquito. This is the first known record of it attacking a species of *Ziziphus*.

ACKNOWLEDGMENTS

The Hymenoptera reared during this study were identified by Dr. P. M. Marsh and Dr. B. D. Burks of the Entomology Research Division, Agricultural Research Service, U. S. Department of Agriculture. Their assistance is gratefully acknowledged.

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SCIENTIFIC NOTE

Discovery of an error in the 1890 description of *Pulverro columbianus* (Kohl) (Hymenoptera : Sphecidae).—A study of the genus *Pulverro* over the past several years has revealed an error in the description of the species *P. columbianus* as published by Kohl in 1890 (K. K. Naturhist. Hofmus. Ann., 5: 61). The 17 specimens of this species available for study are all males and according to the catalog no females have been collected, but yet Kohl's description referred to the holotype as a female. Otherwise his description matches the male specimens in our collections. Kohl's holotype specimen is in Vienna and through the kind assistance of Dr. Max Fischer of the Naturhistorisches Museum it was loaned to me for study. The specimen is in rather poor condition with the head detached and glued to a separate point. The antennae are missing, but the terminal abdominal segments are intact and the specimen is indeed a male, so the 1890 publication is in error and the species *P. columbianus* is known only as males. I have established two homotypes for future reference. Collection data of the specimens studied indicates that the species *P. colorado* Pate is probably synonymous with *P. columbianus* and *P. colorado* has been found to be only females. The species *P. monticola*, which I described in 1968 (Pan-Pac. Entomol., 44: 263), is closely related to *P. columbianus* and the females of *P. monticola* show a definite resemblance to *P. colorado* even though there are specific differences.—LLOYD E. EIGHME, *Pacific Union College, Angwin, California* 94508.